

NEW SPECIES AND PHYLOGENETIC ANALYSIS OF *LOTOPHILA* LIOY (DIPTERA: SPHAEROCERIDAE)

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Abstract

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The Holarctic genus *Lotophila* Lioy is revised. Five species are recognized: *L. atra* (Meigen), *L. confusa* n. sp. (type locality Nuevo Leon, Mexico), *L. pallida* Hayashi, *L. bicolor* n. sp. (type locality Helumbu District, Nepal), and *L. norrbomi* (Papp) n. comb. The latter species is transferred from *Copromyza* Fallén. The synonymy of *Borborus modestus* Meigen, *B. lugens* Meigen, *B. geniculatus* Macquart, and *B. analis* Roser with *L. atra* is confirmed, and *B. aeneus* Macquart is considered a new synonym. Lectotypes are designated for *B. modestus*, *B. geniculatus*, *B. analis*, and *B. aeneus*. Variation among populations of *L. confusa* is described and discussed. Phylogenetic relationships within *Lotophila* and between it and other genera of Copromyzini are analyzed. Illustrations and a key to species are provided.

Introduction

Norrbom and Kim (1984) resurrected the genus *Lotophila* Lioy and analyzed its relationships to other taxa of the subfamily Copromyzinae. They included only one species, *L. atra* (Meigen), which breeds in dung of cattle and other animals and is one of the most common Holarctic species of Sphaeroceridae. Hayashi (1985) described a second species, *L. pallida*, from Japan, and *Copromyza norrbomi* Papp, recently described from India and Nepal (Papp 1988), also belongs in this genus. As part of a comprehensive revisionary study of the Copromyzinae, we describe two additional species of *Lotophila* in this paper, provide a key to all five species, and analyze the phylogenetic relationships within the genus.

Materials and Methods

We follow the morphological terminology of McAlpine (1981) and Marshall and Richards (1987) except as noted. The male sclerite here referred to as synsternite 6+7 has previously been considered by most sphaerocerid workers to be derived only from the sclerites of segment 6. Kim and Cook (1968) called it sternite 6 + tergite 6, whereas Griffiths (1972) interpreted it as sternite 6, with the assumption that the extra spiracle on the left side migrated from sternite 7. Throughout the Sphaeroceridae, this sclerite bears not only the two spiracles on the left side, but also two distinct pairs of sensilla trichodea. These previously overlooked sensilla strongly suggest that this sclerite is synsternite 6+7. It follows from this that the next sclerite, sometimes partially fused with synsternite 6+7, is sternite 8, not sternite 7. The "genital arch" of Norrbom and Kim (1984) therefore can not be a fusion of sternite 8 and the epandrium, and it is here interpreted as just the epandrium. We refer to the parts of the aedeagus according to their actual dorsoventral orientation, which is opposite the original condition in the Diptera due to the fact that the aedeagus is bent forward in the Muscomorpha. The parts of the distiphallus are labelled in figures 6 and 7.

Acronyms for depositories of specimens cited in the text are as follows: Canadian National Collection, Ottawa (CNC); Muséum d'Histoire naturelle de Genève (MHNG); Museum National d'Histoire Naturelle, Paris (MNHN); National Institute of Agricultural Sciences, Tsukuba, Ibaraki-ken, Japan (NIASJ); Naturhistorisches Museum, Wien (NMW); Staatliches Museum für Naturkunde, Stuttgart (SMNS); University of Guelph, Ontario (GUE); National Museum of Natural History, Smithsonian Institution (USNM); Utah State University, Logan (USUL); Zoological Institute, University of Lund (ZIL).

We follow the system of Marshall (1985) to indicate character weighting in the cladogram showing our hypothesis of phylogenetic relationships among the species of *Lotophila* (Fig. 1). Species of the sister group (*Dudaia* Hedicke, *Afroborborus* Curran, *Borborillus* Duda, *Metaborborus* Vanschuytbroeck, and *Gymnotetopina* Hedicke), as well as other Copromyzini (*Crumomyia* Macquart, *Alloborborus* Duda, and *Copromyza* Fallén), were examined for purposes of outgroup comparison.

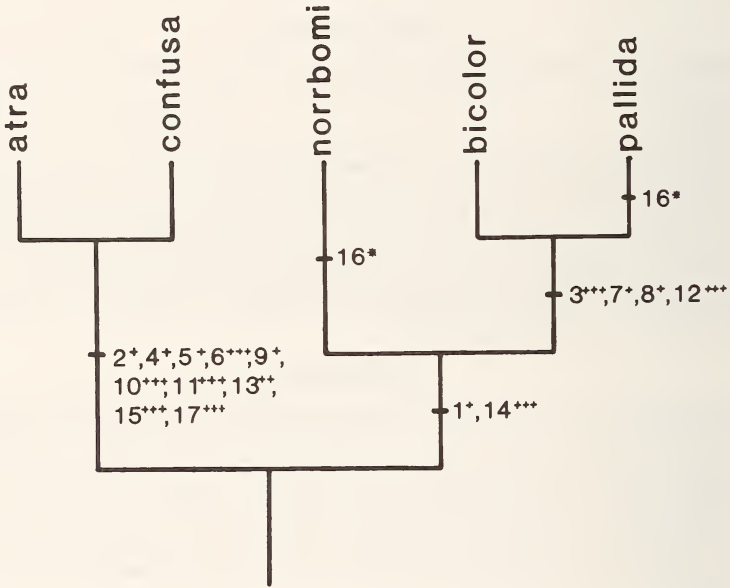


FIGURE 1. Hypothesis of phylogenetic relationships among species of *Lotophila*. Numbers refer to the apomorphic states of characters listed in Tables I and II. Character weighting system follows Marshall (1985). Characters with (+++) are complex, unique or rare in the Copromyzini, and considered unlikely to be the result of homoplasy; characters with (+) are of uncertain polarity or are highly variable in other Copromyzini; and those with (++) are intermediate. Characters with (*) represent homoplasy.

Lotophila Lioy

- (part) *Borborus*; Meigen 1830: 198; Becker 1905: 23.
- Lotophila* Lioy 1864: 1113 (Type species – *Borborus lugens* Meigen, by designation of Richards 1930: 264, = *B. ater* Meigen); Norrbom and Kim 1984: 305; Hayashi 1985: 561; Pitkin 1988: 30; Papp 1988: 466.
- (part) *Olina*; Becker 1905: 27.
- Borborus (Olina)*; Duda 1923: 58, 99.
- Scatophora*; Spuler 1925: 1.
- Copromyza (Olina)*; Richards 1930: 263, 315.
- Borborus (Borborus)*; Duda 1938: 35.
- Copromyza (Olinea)* Richards 1961: 561 (*nomen nudum*).
- Copromyza (Olinea)* Richards 1965: 719 (Type species – *Borborus ater* Meigen, by original designation).
- Copromyza (Lotophila)*; Papp 1984: 74.

Diagnosis. Differing from all other Copromyzini except *Achaetothorax* Hedicke by the absence

of a ventroapical spur on the hind tibia. *Lotophila* is easily distinguished from *Achaetothorax* by the lack of rows of stout, spinelike ventral setae on the hind femur, and in having the scutum entirely microtrichose.

Description. Mostly black, 2.4-4.0 mm long. Head – largely microtrichose, subquadrate; frons yellow or orange anteriorly; genal seta small; ocellar setae posterior to median ocellus; postocular setae in single row. Thorax – scutum and scutellum entirely microtrichose, but varying in density giving appearance of faint stripes between acrostichal and dorsocentral setae; acrostichal setae in 2 rows, often a few additional setae posteriorly; usually 3 (1+2) dorsocentral macrosetae, but anterior 2 often poorly or sometimes not at all differentiated; scutellum with 2-5 pairs of marginal setae, if more than 2, all stout and subequal; katapisternum without dorsal macroseta. Legs – mid tibia with whorl of small preapical setae, usually with 1-2 small anterior setae and often 1 small posteroventral seta between basal 2/5 and 3/4; hind tibia with small preapical dorsal seta, without ventroapical spur or anteroventral seta; male fore and hind metatarsi without hooklike apical spurs. Wing – cell dm elongate, crossvein dm-cu in apical third of wing; vein M extending to wing margin; vein Cu₁ ending short distance beyond dm-cu, not extending to margin; crossveins r-m and dm-cu unbanded; r-m at 1/3 to 1/2 distance from bm-cu to dm-cu. Male abdomen – synsternite 6-7 without posterior median lobe, membrane posterior to its right tip often sclerotized and sometimes fused to synsternite; epandrium usually without lateral cleft; hypandrial apodeme greatly reduced; cerci fused to epandrium; postphallic sclerite present between basiphallus and interparameral sclerite (sternite 10); basiphallus with epiphallus reduced but with median ventral apodeme (preepiphallus); distiphallus with the following: transverse medial sclerite dorsobasally, usually with 2 lateral lobes; slender elongate dorsomedial sclerite; pair of multitoothed, dorsally projecting lateral sclerites; and pair of large lateral sclerites, strongly sclerotized basally, less so in apical half, and with subapical hook or acute apex. Female abdomen – terminalia long and telescoping; 2 spermathecae, apodeme opposite duct opening small, its apex membranous.

Remarks. Spuler (1925) considered *Scatophora* Robineau-Desvoidy (1830) to be the valid name for this genus, and its type species, *S. carolinensis* Robineau-Desvoidy (by designation of Spuler 1925), to be the valid name for the species we recognize as *L. atra* (Meigen) (Robineau-Desvoidy 1830 was published earlier in the year than Meigen 1830). This synonymy is doubtful, as Spuler based it only on Robineau-Desvoidy's description of *Scatophora* as having the hind tibia without an apical spine. As indicated by Duda (1938), Robineau-Desvoidy also stated that *S. carolinensis* was "2 lignes 1/3" (approximately 4.9 mm) long, whereas *L. atra* is never more than 4.0 mm in length. Robineau-Desvoidy's statements "pattes entremêlées de noirâtre et de fauve" (legs of intermixed blackish and tawny) and "ailes assez fuligineuses" (wings rather fuliginous) also do not fit *L. atra*. Because their descriptions are so brief and the types are apparently lost (there are no sphaerocerid types in the Robineau-Desvoidy collection in the MNHNP), it is unlikely that *Scatophora* and the other Robineau-Desvoidy names attributed to the Sphaeroceridae (see Papp 1984) will ever be recognized.

Relationships to other Copromyzini. *Lotophila* is the sister group of a monophyletic group that includes *Gymnometopina* Hedicke, *Metaborborus* Vanschuytbroeck, *Dudaia* Hedicke, *Afroboborus* Curran (Norrbon and Kim 1984, 1985), and *Borborillus* Duda (at least *B. uncinatus* (Duda) and *B. vitripennis* (Meigen)). The latter five genera share at least two synapomorphies: 1) male abdominal synsternite 6-7 with a medial posterior lobe; and 2) the male cerci separated from the epandrium. *Lotophila* shares with these taxa the following apomorphies of the male terminalia: 1) the presence of a postphallic sclerite between the basiphallus and the interparameral sclerite (sternite 10); and 2) the epandrium (genital arch) without lateral clefts. The only male specimen of *L. norrboni* that we have examined has what appears to be a cleft on the right side of the epandrium, but because the left side is entirely fused and no clefts are present in the other species of *Lotophila*, we continue to regard their loss, at least on the left side, as a synapomorphy. Norrbom and Kim (1984) also stated that the cerci were partially cleft from the epandrium in *L. atra* and that this partial separation could be interpreted as an additional synapomorphy. Reexamination of this structure in *L. atra* and *L. confusa* indicates that what Norrbom and Kim interpreted as a cleft is an internal ridge. The cerci are fused to the epandrium (the plesiomorphic state) in all species of *Lotophila*.

Probable synapomorphies indicating the monophyly of *Lotophila* include the loss of the ventroapical spur on the hind tibia, the shape of the dorsally projecting sclerites of the distiphallus, and the presence of the ventral medial apodeme on the basiphallus. The loss of the spur on the hind tibia in *Achaetothorax* and *Lotophila* clearly occurred independently, as indicated by numerous synapomorphies each taxon shares with other genera. Sclerites that are possibly homologous with the dorsally projecting sclerites of the distiphallus of *Lotophila* are present in most *Gymnometopina*, *Dudaia*, and *Metaborborus* species, but they are shorter and do not have as many teeth as in *Lotophila*. In the outgroup, except in some species of *Crumomyia* Macquart and *Dudaia*, the basiphallus does not have a ventral medial apodeme. We tentatively hypothesize that the occurrence of the apodeme in these other two genera is the result of homoplasy.

TABLE I. Characters and character states used in phylogenetic analysis of the species of *Lotophila*. Character state 0 is hypothesized as plesiomorphic and state 1 as derived unless otherwise stated.

1. Face microtrichial pattern – 0) entirely microtrichose; 1) lower corners with bare spot. Variable in outgroup, polarity is uncertain.
2. Frons microtrichial pattern – 0) entirely microtrichose; 1) with large medial bare area(s).
3. Anterior fronto-orbital seta – 0) more than half as long as posterior seta; 1) reduced, about 1/3 as long as posterior seta or absent.
4. Anepimeron microtrichial pattern – 0) entirely microtrichose; 1) largely bare.
5. Meron microtrichial pattern – 0) microtrichose, at least medially; 1) often with medial bare spot.
6. Scutellar marginal bristles – 0) 2 pairs; 1) 4-5 pairs.
7. Fore coxa color – 0) at least base dark brown to black; 1) entirely yellow. Variable in outgroup, polarity is uncertain.
8. Femora color – 0) mostly black, at least basally; 1) mostly yellow, with apices sometimes dark brown. Variable in outgroup, polarity is uncertain.
9. Fore femur microtrichial pattern – 0) entirely microtrichose; 1) with large posterior bare area. Variable in outgroup, polarity is uncertain.
10. Male sternite 5 – 0) without apodeme or with symmetrical basal apodeme; 1) with asymmetrical basal apodeme, more well developed on left side.
11. Epandrium – 0) not expanded anterodorsally; 1) expanded anterodorsally.
12. Cercus – 0) well developed; 1) small, poorly differentiated from epandrium.
13. Surstylus – 0) anterior and ventral or posteroventral margins not forming strongly acute angle; 1) anterior and posteroventral margins forming sharply acute angle.
14. Dorsally projecting sclerites of distiphallus – 0) slender, straight, with small apical teeth; 1) broad, curved, with large marginal and apical teeth.
15. Lateral sclerite of distiphallus – 0) strongly sclerotized part short, gradually curved dorsally, or entirely straight; 1) strongly sclerotized part elongate, straight, with apex turned dorsally.
16. Lateral sclerite of distiphallus – 0) strongly sclerotized part without apical teeth; 1) strongly sclerotized part with at least 2 apical teeth.
17. Paramere – 0) apical lobe without large lateral lobe; 1) apical lobe with large lateral lobe.

Relationships within *Lotophila*. Tables I and II list the characters and their states that we consider relevant for the analysis of the phylogenetic relationships within *Lotophila*. Characters also analyzed but considered autapomorphic for particular species include the following: *L. atra* – female abdominal sternite 4 weakly sclerotized; *L. norrbomi* – meron almost entirely bare, basal sclerite of distiphallus with lateral lobes poorly developed, medial sclerite of distiphallus with subapical lobes, lateral sclerite of distiphallus with large dentate lobes at apex of strongly sclerotized part; *L. bicolor* – epandrium posterodorsally expanded, medial sclerite of distiphallus forked apically; *L. pallida* – anepisternum entirely microtrichose, female abdominal sternites 2-4 weakly sclerotized, male abdominal sternites 2-3 weakly sclerotized, male abdominal sternite 5 with a symmetrical basal apodeme.

The most parsimonious cladogram based on the characters of Tables I and II is represented in Fig.

TABLE II. Character state distributions in the species of *Lotophila*.

Character	<i>atra</i>	<i>confusa</i>	<i>norrbomi</i>	<i>bicolor</i>	<i>pallida</i>
1	0	0	1	1	1
2	1	1	0	0	0
3	0	0	0	1	1
4	1	1	0	0	0
5	1	1	0	0	0
6	1	1	0	0	0
7	0	0	0	1	1
8	0	0	0	1	1
9	1	1	0	0	0
10	1	1	0	0	0
11	1	1	0	0	0
12	0	0	0	1	1
13	1	1	0	0	0
14	0	0	1	1	1
15	1	1	0	0	0
16	0	0	1	0	1
17	1	1	0	0	0

1. Several obvious apomorphies suggest that *L. atra* and *L. confusa* form a monophyletic subgroup, which is probably the sister group of the other three species. Of those three, *L. bicolor* and *L. pallida* appear more closely related. *Lotophila norrbomi* might be more closely related to *L. atra* and *L. confusa* than to *L. bicolor* and *L. pallida*, especially if we interpreted the polarities of characters 1, 7 and 8 incorrectly. These characters involve color and microtrichial patterns, which vary greatly in the Copromyzini, and we consider them more subject to homoplasy than character 14, a complex structural character. We interpret the presence of a symmetrical basal apodeme on male sternite 5 in *L. pallida* as an independently derived character state rather than a synapomorphy that *L. pallida* shares with *L. atra* and *L. confusa*, which have an asymmetrical apodeme, because of the different shapes of the apodemes and because of the distribution of other character states. Character 16, which suggests a closer relationship between *L. norrbomi* and *L. pallida*, is here considered the result of homoplasy.

Key To The Species Of *Lotophila*

- 1. Scutellum with 4-5 pairs of marginal setae; frons with large shiny bare area medially (Fig. 2A-B); anepimeron largely bare, shiny (Fig. 2C-D); fore femur with large posterior shiny area 2
- Scutellum with 2 pairs of marginal setae; frons, anepimeron (Fig. 3), and fore femur entirely microtrichose 3
- 2. Bare shiny area of frons usually divided into 3 parts (Fig. 2B); fore coxa entirely dark brown; female abdominal sternite 4 as strongly sclerotized as other sternites; distiphallus of male

- (Fig. 6B-D) with apex of weakly sclerotized apical part of lateral sclerite strongly acute, ending close to medial sclerite; apex of strongly sclerotized basal part of lateral sclerite gradually dorsally curved *confusa* n. sp.
 Bare shiny area of frons undivided (Fig. 2A); fore coxa usually with at least apex yellow; female abdominal sternite 4 weakly sclerotized, poorly differentiated from pleural membrane; distiphallus (Fig. 6A) with weakly sclerotized apical part of lateral sclerite with acute subapical lobe far removed from medial sclerite; apex of strongly sclerotized basal part of lateral sclerite sharply dorsally turned *atra* (Meigen)
3. Hind femur mostly dark brown or black, sometimes with yellow spot or band subapically; meron (Fig. 3A) mostly bare, shiny; distiphallus with apex of strongly sclerotized basal part of lateral sclerite elongate, multitoothed, resembling dorsally projecting sclerite (Fig. 6E); distiphallus with basal sclerite broad, platelike, with lateral lobes very small (Fig. 7B) *norrboni* (Papp)
 Hind femur yellow with apical 1/4 to 1/5 dark brown; meron (Fig. 3B) microtrichose, dull; distiphallus with apex of strongly sclerotized basal part of lateral sclerite at most with 2 teeth, not projecting dorsally (Fig. 6F-G); distiphallus with basal sclerite narrower, with lateral lobes large (Fig. 7C-D) 4
4. Anepisternum entirely microtrichose, dull; abdominal sternites 2-3 of male and 2-4 of female weakly sclerotized; surstylus (Fig. 5F-G) elongate, only slightly wider at apex than at base; distiphallus (Fig. 6F, 7C) with medial sclerite simple, not forked apically *pallida* Hayashi
 Anepisternum (Fig. 3B) mostly bare, shiny, except narrowly microtrichose along dorsal margin and in lower posterior corner; all abdominal sternites of male strongly sclerotized, female unknown; surstylus (Fig. 4C) triangular, much broader apically than at base; distiphallus (Fig. 6G, 7D) with medial sclerite forked apically *bicolor* n. sp.

Lotophila atra (Meigen)

(Fig. 2A,C, 4A, 5A-B, 6A, 7A, 8A)

- Borborus ater* Meigen 1830: 203 (Lectotype ♂ (NMW), "Von Hm. von Winthem", locality not stated, probably W. Germany: Hamburg (see Pont 1986); designated by Norrbom and Kim 1984: 307).
- Borborus modestus* Meigen 1830: 203 (Lectotype ♂ (NMW), France: Montpellier, Winthem; here designated).
- Borborus lugens* Meigen 1830: 205 (Lectotype ♀ (NMW), France: region of Lyon, Winthem; designated by Norrbom and Kim 1984: 307).
- Borborus geniculatus* Macquart 1835: 567 (Lectotype ♂ (MNHNP), France; here designated).
- Borborus analis* Roser 1840: 64 (Lectotype ♂ (SMNS), W. Germany: Würtemberg; here designated).
- Borborus aeneus* Macquart 1849: 500 (Lectotype ♂ (MNHNP), Algeria: environs of Algiers or Constantine, IV, Lucas; here designated). n. syn.
- Lotophila lugens*; Lioy 1864: 1113.
- Olina geniculata*; Becker 1905: 27.
- Olina ferruginea* Becker 1908: 198 (Holotype ♂ (probably Zoological Museum, Humboldt Universität, Berlin), Madeira; not examined, synonymy following Duda 1938: 36).
- Borborus (Olina) geniculata*; Duda 1923: 99.
- Scatophora carolinensis*; Spuler 1925: 1.
- Copromyza (Olina) hirtipes*; Richards 1930: 315.
- Borborus (Borborus) ater*; Duda 1938: 35.
- Copromyza (Olinea) atra*; Richards 1961: 562, 1965: 719.
- Lotophila atra*; Norrbom and Kim 1984: 306 (in part); Hayashi 1985: 563; Pitkin 1988: 30; Papp 1988: 466.
- Copromyza (Lotophila) atra*; Papp 1984: 74.

Description. 2.5-4.0 mm long. Head – frons with anterior yellow or orange area usually discrete,

narrow and transverse or, if broader, M-shaped; frons with broad medial bare shiny area extending posteriorly lateral to ocelli (Fig. 2A); anterior fronto-orbital seta about half as long to subequal to posterior seta; gena bare except anterior and extreme ventral margins; face entirely microtrichose. Thorax (Fig. 2C) – with following areas bare and shiny: postpronotal lobe laterally and often posterodorsally, anepisternum except upper posterior corner, anterior 3/5 of anepimeron, katepisternum except posterior dorsal margin and narrowly along sternal suture; meron often with medial bare spot; scutellum with 4-5 pairs of short stout marginal setae, apical pair slightly longer. Legs – femora and tibiae blackish except extreme bases and apices yellow; fore coxa usually with at least apex yellow; fore femur with large posterior shiny area without microtrichia. Male abdomen – sternites 2-5 strongly sclerotized; sternite 5 irregular, shaped like broad inverted U, basally with broad apodeme more strongly developed on left side; epandrium (Fig. 4A) relatively small but expanded anterodorsally, without lateral cleft; cercus well developed; surstylus (Fig. 5A-B) triangular, anterior margin concave and forming acute angle with posteroventral margin, the latter not strongly concave subapically; paramere (Fig. 8A) with short anterior lobe, apical lobe with large lateral lobe; distiphallus (Fig. 6A, 7A) with transverse basal sclerite moderately broad, its lateral lobes well developed; dorsally projecting sclerite slender, almost straight, with only apical teeth; lateral sclerite with apex of strongly sclerotized part acute, sharply turned dorsally, weaker apical part with subapical acute lobe well separated from medial sclerite; medial sclerite simple. Female abdomen – sternite 4 weakly sclerotized, poorly differentiated from pleural membrane.

Distribution. Middle latitudes of Holarctic Region. See Norrbom and Kim (1984) for more detailed data (but note that the records from Tibet, Arizona, and Mexico apply to *L. confusa*). Papp (1988) also reported this species from northern Pakistan.

Remarks. Norrbom and Kim (1984) included within *L. atra* several populations that we recognize here as a distinct species, *L. confusa*.

All of the putative type specimens discussed in this section, including the paralectotypes, are *L. atra*. The Meigen specimens from the NMW generally have the same types of labels. 1) a small label with the species name in Meigen's writing, as verified by Dr. Ruth Lichtenberg, curator of the NMW Diptera collection. 2) a label with "Coll. Winth." in machine printing and a species name in freehand; these were added when the Winthem Collection was incorporated into the NMW general collection; the writing is of a museum worker at that time, it is not Duda's as stated by Norrbom and Kim (1984). 3) a red "TYPE" label, also not original; the holotype of *Borborus clunicrus* Duda (1923) has such a label, thus they may have been added after this date.

The lectotype and 5♂ paralectotypes of *B. ater* each have a "Coll. Winth., ater" label, a red "TYPE" label, and a label with "Oolina geniculata" in Duda's writing. The lectotype of *B. modestus* has the following labels: "Montpellier" in freehand; "modestus" in Meigen's writing; "Coll. Winth., modestus"; "geniculatus Macq." in Duda's writing; and a red "TYPE" label. The lectotype of *B. lugens* has labels with "lugens" in Meigen's writing, "Coll. Winth., lugens", "geniculata Macq. d. Duda" in Duda's writing, and a red "TYPE" label. The lectotype of *B. analis* has labels with "Borborus analis, m." in what is probably Roser's writing, "Borboris analis R. 35.", and a Becker determination label with "Oolina geniculata Meig". Only single putative syntypes of each of the last 3 species were found, but because Meigen and Roser did not state the number of specimens they had, we have designated these specimens as lectotypes.

There are two male syntypes of *B. geniculatus* in Box 8 of the Macquart Collection in the MNHNP. Both have labels with "MUSEUM PARIS, Lille, Macquart". The lectotype also has a label with "Borborus geniculatus" in Macquart's writing and one with "970". The paralectotype has a label with "M: 102 Borborus geniculatus" in Macquart's writing. There is also a male that we do not consider a paralectotype with a label with "Borborus geniculatus ?" in Macquart's writing. Macquart's personal collection in Lille may contain additional paralectotypes; he mentioned females as well as males in the description. Macquart (1849) stated that the types of *B. aeneus* were female, but this is probably an error because his figure (Pl. 6, Fig. 12) is of a male, and the 3 putative syntypes of *B. aeneus* in the Macquart Collection of the MNHNP, in a box labelled "No. 6, Mission H. Lucas, Algérie", are males. All 3 have machine printed labels with "MUSEUM PARIS, ALGERIE, COLL. H. LUCAS 78-49". The lectotype also has a blue label with "270", matching the number for this

species in Macquart (1849), and a label with "Borborus aeneus Macqt. sp. nov." in Macquart's writing. One paralectotype also has a blue label with "270" and a label with "Borborus aeneus Macqt."; the other has a blue label with "437". Macquart's figure shows the hind tibia with an apical spur, but this is probably an error because the legs are obviously stylized; the fore tibiae have apical spurs, which are never present in Copromyzinae, and the tarsi, especially the hind metatarsi, are inaccurate for any sphaerocerid.

Specimens examined. Lectotypes of *B. ater*, *B. modestus*, *B. lugens*, *B. analis*, *B. geniculatus*, and *B. aeneus*; 5♂ paralectotypes of *ater*, 1♂ paralectotype of *B. geniculatus*, and 2♂ paralectotypes of *B. aeneus* (see "Remarks"). We have examined over 800 specimens, the complete data for which we will not list here. Many were previously listed by Norrbom and Kim (1984). These included Nearctic specimens from the Canadian provinces of British Columbia, Alberta, Ontario, Quebec, New Brunswick, Nova Scotia, and Newfoundland, and all states of the United States except N. Dakota, Wyoming, Utah, Nevada, Delaware, Kentucky, Mississippi, Alabama, Louisiana, Texas, Arizona, Alaska, and Hawaii. We have also seen Palaearctic specimens from Norway, Sweden, Denmark, England, Scotland, The Netherlands, Belgium, France, W. Germany, Switzerland, Austria, Spain, Rumania, the Soviet Union (Uzbek), Crete, Morocco, Algeria, and the Azores.

TABLE III. Characters varying among populations of *L. confusa* and *L. atra*.

- 18. Frons microtrichial pattern – a) with 3 bare areas; b) with 1 bare area.
- 19. Color of fore coxa – a) partly yellow; b) entirely dark.
- 20. Strongly sclerotized part of lateral sclerite of distiphallus – a) apex sharply turned; b) apex gradually curved.
- 21. Weakly sclerotized part of lateral sclerite of distiphallus – a) with apical hooks far from medial sclerite; b) with apex acute, ending at medial sclerite; c) with apex acute, extending beyond medial sclerite.
- 22. Anepisternum microtrichial pattern – a) dorsal margin microtrichose; b) only posterior corner microtrichose.
- 23. Postpronotal lobe microtrichial pattern – a) entirely microtrichose; b) with a small lateral bare spot; c) with a large lateral and dorsal bare spot.
- 24. Surstylus – a) posteroventral margin convex or slightly concave subapically; b) posteroventral margin strongly concave subapically.

TABLE IV. Character state distributions in populations of *L. confusa* and *L. atra*.

Character	<i>atra</i>	<i>confusa</i> Mexico	<i>confusa</i> Arizona	<i>confusa</i> Alaska	<i>confusa</i> China
18	b	a (rarely b)	a	a (rarely b)	a
19	a (rarely b)	b	b	b	b
20	a	b	b	b	b
21	a	b	b	b	c
22	b	a	b	b	a
23	c	a/b	b	b	a
24	a	b	b	b	a

Lotophila confusa n. sp.
(Fig. 2B,D, 5C-E, 6B-D, 8B)

(part) *Lotophila atra*; Norrbom and Kim 1984: 306.

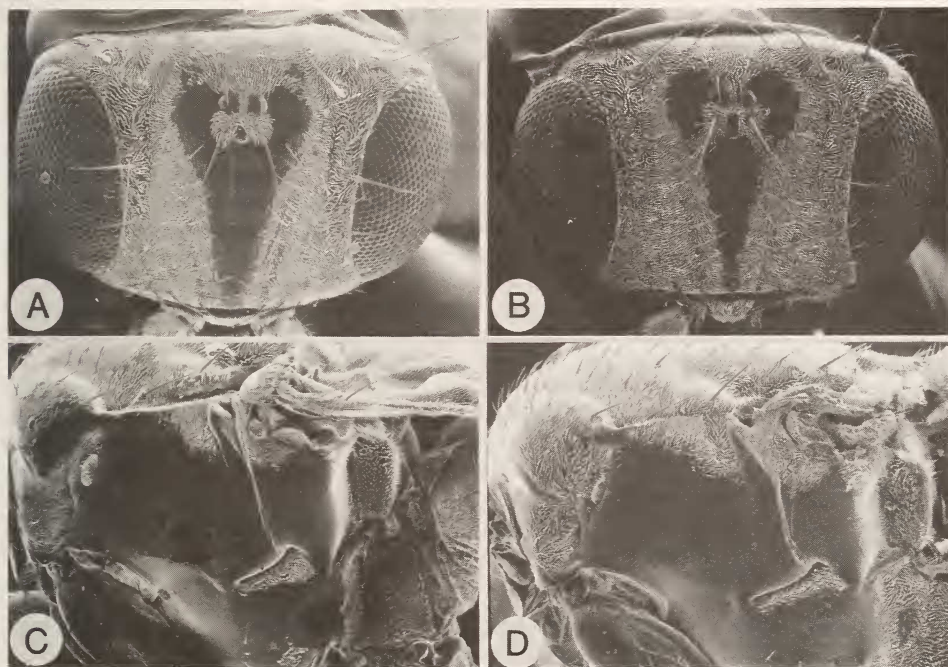


FIGURE 2. Scanning electron photomicrographs: A, C – *L. atra*, U.S.A., Virginia; B, D – *L. confusa*, Mexico, Mexico; A, B – head, dorsal view; C, D – thorax, left lateral view.

Description. 2.7-3.5 mm long. Head – frons with anterior yellow or orange area usually discrete, narrow and transverse or, if broader, M-shaped; frons usually with 3 bare shiny areas, 1 medially and 1 on each side of ocelli (Fig. 2B), these rarely connected; anterior fronto-orbital seta about half as long to subequal to posterior seta; gena bare except anterior and extreme ventral margins; face entirely microtrichose. Thorax – with following areas bare and shiny: anepisternum except upper posterior corner and sometimes (specimens from Mexico and China) dorsal margin (Fig. 2D), anterior 3/5 of anepimeron, katepisternum except posterior dorsal margin and narrowly along sternal suture; meron often with medial bare spot; postpronotal lobe sometimes with small lateral bare spot but never bare dorsally; scutellum with 4-5 pairs of short stout marginal setae, apical pair slightly longer. Legs – femora and tibiae blackish except extreme bases and apices yellow; fore coxa entirely dark brown to black; fore femur with large posterior shiny area without microtrichia. Male abdomen – sternites 2-5 strongly sclerotized; sternite 5 irregular, shaped like broad inverted U, basally with broad apodeme more strongly developed on left side; epandrium (similar to Fig. 4A) relatively small but expanded anterodorsally, without lateral cleft; cercus well developed; surstylus (Fig. 5C-E) triangular, anterior margin concave and forming acute angle with posteroventral margin, the latter strongly concave subapically (except in specimen from China, Fig. 5C); paramere (Fig. 8B) with short anterior lobe, apical lobe with large lateral lobe; distiphallus (Fig. 6B-D) with transverse basal sclerite moderately broad,

its lateral lobes well developed; dorsally projecting sclerite slender, almost straight, with only apical teeth; lateral sclerite with apex of strongly sclerotized part acute, gradually dorsally curved, weaker apical part with apex strongly acute, elongate, extending to or (in specimen from China, Fig. 6D) slightly beyond medial sclerite; medial sclerite simple. Female abdomen – sternites 2-5 strongly sclerotized.

Distribution. Highlands of northern and central Mexico, Arizona, and Szechwan; Alaska at lower elevations. Probably also occurring in Rocky Mountains and more extensively, especially at high elevations, in the eastern Palaearctic Region.

Remarks. The populations that we recognize here as *L. confusa* present an interesting systematic problem. Norrbom and Kim (1984) indicated that specimens examined from China, Arizona, and Mexico differed in some respects from typical *L. atra*, but treated them as that species. Discovery of additional material, especially the Alaskan population, and additional study indicates that they represent at least one distinct species. These populations differ consistently from *L. atra* in the shape of the apices of both the strongly and weakly sclerotized parts of the lateral sclerite of the distiphallus, the sclerotization of female sternite 4 (at least in females from Mexico and Alaska, none are known yet from Arizona or China), usually the color of the fore coxa (which varies in *L. atra*), and usually the microtrichial pattern of the frons, in which the bare area is divided (except in 1 of 33 specimens from Mexico and 3 of 17 from Alaska).

The variation in several characters among these populations and *L. atra* is shown in Tables III and IV. The specimens from Alaska and Arizona are most similar, which suggests that additional populations of *L. confusa* may occur in the Rockies. The specimen from China differs most in the characters of the male genitalia, but it and specimens from Mexico have the most similar microtrichial patterns, with the entire dorsal margin of the anepisternum microtrichose and usually the postpronotal lobe entirely microtrichose. Some specimens from northern Mexico have a small lateral bare spot on the postpronotal lobe. The Mexican, Arizonan, Alaskan, and especially the Chinese populations may eventually prove to represent different species, but given the number of specimens on hand, their geographic distributions, and the character state distributions among them, we believe it is untenable to recognize them as such at this time.

Etymology. The name of this species is derived from the Latin “confusio” which refers to its previous taxonomic status.

Holotype. (CNC), MEXICO: Nuevo Leon, E slope Cerro Potosí, 9200 ft, “human dung”, V.1971, A. Newton.

Paratypes. All from Mexico. Same data as holotype, 3♂1♀ (GUE), 2 (USNM); Nuevo Leon, Cerro Potosí, NW of 18 de Marzo, 3000 m., 27.VI.1986, M. Sörensson and B. Mårtensson, 2♂ (ZIL) 1♂1♀ (USNM); Durango, El Salto, 4.VIII.1971, D. W. Davis, 2♂6♀ (USUL), 1♂2♀ (USNM); Veracruz, 21 mi. W of Orizaba, 4.IX.1974, W. Hanson and G. Bohart, 1♂ (USNM); Mexico, 10 mi. E of Toluca, 8900 ft., 31.VII.1954, J. G. Chillcott, 4♂2♀ (CNC), 2♂2♀ (USNM); Popocateptl, 12,000 ft., 11.VIII.1938, G. O. Lee, 1 specimen without abdomen (USNM).

Additional specimens examined. UNITED STATES: Arizona: White Mts., Coulter Ranch, 9200 ft., 28.VI.1947, J. L. Sperry, 1♂ (USNM); Alpine, 23.VI.1947, J. L. Sperry, 1♂ (USNM); Alaska: Richardson Hwy., km. 206, dung traps and sweeping, 9-20.VI.1987, S. A. Marshall, 8♂4♀ (GUE), 2♂2♀ (USNM); Richardson Hwy., 20 mi. S of Delta Jct., Donnelly Dome, dung trap, 20.VIII.1985, S. A. Marshall, 1♂ (GUE); CHINA: “Tibet border, Yu-Long-Gong” [Szechwan, U Long Kong, nr. Tatsienlu (= Kangding), approx. 200 km E Tibet border], 14,000 ft., 14.VIII.1930, D. C. Graham, 1♂ (USNM).

Lotophila norrbomi (Papp), n. comb.

(Fig. 3A, 4B, 6E, 7B, 8C)

Copromyza norrbomi Papp 1988: 467 (Holotype ♂ (MHNG), INDIA: W. Bengal, Darjeeling Dist., Tonglu, 3100 m, 16.X.1978, C. Besuchet & I. Löbl).

Description. 3.3-3.8 mm long. Head – frons entirely microtrichose, with anterior yellow or

orange area discrete, usually M-shaped; anterior fronto-orbital seta slightly more than half as long as posterior seta; genal bare area T-shaped, at midpoint height of microtrichose area about 2/3 that of bare area; face microtrichose except large bare spot in each lower corner. Thorax (Fig. 3A) – postpronotal lobe and anepimeron entirely microtrichose; anepisternum bare except very narrowly along dorsal and posterior margins; meron bare except dorsally; katapisternum bare except posterior half of dorsal margin and narrowly along sternal suture; scutellum with 2 pairs of marginal setae, basal pair smaller than apical pair. Legs – femora black, at least basally; hind femur entirely black except for ventral spot or complete band of yellow or orange at 4/5; fore coxa entirely black; fore femur entirely microtrichose. Male abdomen – sternites 2-5 strongly sclerotized; sternite 5 rounded basally, without apodeme, posterior corners not strongly narrowed; epandrium (Fig. 4B) relatively small, not unusually expanded, with lateral cleft only on right side; cercus well developed; surstylus triangular, anterior margin convex; paramere (Fig. 8C) with strong posterior bend and with subapical cluster of medial setae; distiphallus (Fig. 6E, 7B) with transverse basal sclerite broad, platelike, its lateral lobes minute; dorsally projecting sclerite broad, strongly dorsolaterally curved, with large apical and subapical teeth; lateral sclerite with strongly sclerotized part short, with broad strongly dentate dorsally curved apical lobe, weaker apical part slender, elongate; medial sclerite with pair of small subapical lobes. Female abdomen – sternites 2-5 strongly sclerotized.

Distribution. This species is known only from the mountains south of the Himalayas. The type locality is in northeast India, in a district between Nepal, Sikkim, and Bhutan. Papp (1988) also reported a male from Nepal and the specimens we examined came from that country.

Remarks. We have not examined the holotype, but Papp's description, especially of the color of the legs and the microtrichial pattern of the anepisternum, and his figure of the distinctive distiphallus suggest that the specimens we examined are conspecific with it. In Papp's figures, the surstylus is more rounded posteriorly and the paramere is slightly differently shaped than in the male we examined. These apparent differences may be due to variation in these characters or they may be the result of slight differences in orientation when the specimens were drawn. Papp placed this species in *Copromyza*, although he stated that there are no small marginal scutellar setae on the type, and his figure of the genitalia shows no lateral cleft on the left side of the epandrium. Both of these characters are present in *Copromyza*. He did not mention the postphallic sclerite or the hind tibial spur in the description, but the former presumably is present, and the latter absent in the holotype, as in the specimens examined and the other species of *Lotophila*.

Specimens examined. Nepal: 28°00'N, 85°00'E [Helumbu District], 10,500 ft., Malaise trap 6, 26.V.1967, Canadian Nepal Expedition, 1♂ (CNC); same, except date 20.V.1967, 1♀ (CNC); same, except date 1.VI.1967, 1♀ (GUE) 1♀ (USNM).

Lotophila pallida Hayashi

(Fig. 5F-G, 6F, 7C, 8D)

Lotophila pallida Hayashi 1985: 561 (Holotype ♂ (NIASJ), Japan: Hokkaido, Oshima, Nanae, 22.VIII.1982, T. Hayashi).

Description. 2.5-4.0 mm long. Head – frons entirely microtrichose, with anterior yellow or orange area broad, diffuse; anterior fronto-orbital seta absent; genal bare area triangular, its anterior margin well posterior to genal seta; face microtrichose except small bare spot in each lower corner. Thorax – postpronotal lobe, anepisternum, anepimeron, and meron entirely microtrichose; only katapisternum, except dorsal margin and narrowly along sternal suture, bare and shiny; scutellum with 2 pairs of marginal setae, basal pair smaller than apical pair. Legs – femora mostly yellow, apical 1/4 of hind femur and sometimes apices of fore and mid femora dark brown; fore coxa entirely yellow; fore femur entirely microtrichose. Male abdomen – sternites 2-3 weakly sclerotized, sternites 4-5 strong; sternite 5 trapezoidal, with posterior corners strongly narrowed, basally with broad symmetrical apodeme; epandrium large, but normal in shape, without lateral cleft; cercus small, poorly differentiated from epandrium; surstylus (Fig. 5F-G) elongate, only slightly wider apically than basally; paramere (Fig. 8D) with large anterior lobe; distiphallus (Fig. 6F, 7C) with transverse basal sclerite

moderately broad, its lateral lobes well developed; dorsally projecting sclerite moderately broad, slightly curved, with large apical and subapical teeth; lateral sclerite with 2 large spinelike teeth at apex of strongly sclerotized part, weaker apical part slender, elongate, with fine marginal dentitions; medial sclerite simple. Female abdomen – sternites 2-4 weakly sclerotized, sternite 5 strong.

Distribution. Known only from Japan.

Specimens examined. JAPAN: Hokkaido, Nanae, 20.VIII.1982, T. Hayashi, 1♂1♀ paratype (USNM); Honshu, Tokyo, Mt. Takao, 22.VI.1983, T. Hayashi, 1♂1♀ paratype (USNM); Shikoku, Ishizuchi Mt. Nat'l. Park, Tsuchigoya, 1400 m., 11-18. VIII. 1980, S. Peck, 3♂2♀ (GUE), 2♂1♀ (USNM).

***Lotophila bicolor* n. sp.**

(Fig. 3B, 4C, 6G, 7D, 8E)

Description. 3.3-4.0 mm long. Head – frons entirely microtrichose, with anterior yellow or orange area broad, diffuse; anterior fronto-orbital seta small, about 1/3 length of posterior seta; genal bare area subtriangular, its anterior margin near genal seta; face microtrichose except large bare spot in each lower corner. Thorax (Fig. 3B) – postpronotal lobe, anepimeron, and meron entirely microtrichose; anepisternum bare except narrowly along dorsal margin and in lower posterior corner; katepisternum bare except posterior half of dorsal margin and narrowly along sternal suture; scutellum with 2 pairs of marginal setae, basal pair smaller than apical pair. Legs – femora mostly yellow, apical 1/5 of hind femur and sometimes apices of fore and mid femora dark brown; fore coxa entirely yellow; fore femur entirely microtrichose. Male abdomen – sternites 2-5 strongly sclerotized; sternite 5 subrectangular, its posterior corners not strongly narrowed, basally without apodeme; epandrium (Fig. 4C) large, strongly expanded posterodorsally, without lateral cleft; cercus small, linear, poorly differentiated from epandrium; surstylus triangular, its anterior margin concave and forming almost right angle with ventral margin; paramere (Fig. 8E) trilobed apically, posterior margin with minute spines; distiphallus (Fig. 6G, 7D) with transverse basal sclerite narrow, its lateral lobes well developed; dorsally projecting sclerite broad, strongly dorsomedially curved, with numerous marginal teeth; lateral sclerite without teeth at apex of strongly sclerotized part, weaker apical part slender, elongate; medial sclerite forked apically. Female unknown.

Distribution. Known only from the type locality in Nepal.

Etymology. The name of this species is derived from the Latin “bi” and “color”, in reference to the color of the hind femur.

Holotype. ♂ (CNC), Nepal: 28°00' N, 85°00' E. [Helumbu District], 10,500 ft., Malaise trap 6, 1.VI.1967, Canadian Nepal Expedition.

Paratypes. Same data as holotype, except date 26.V.1967, 1♂ (GUE); same, except date 22.V.1967, 1♂ (USNM).

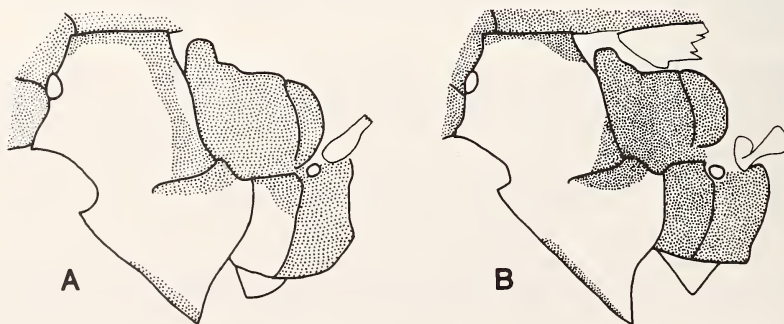


FIGURE 3. Thorax, left lateral view: A – *L. norrbomi*, Nepal; B – *L. bicolor*, Nepal.

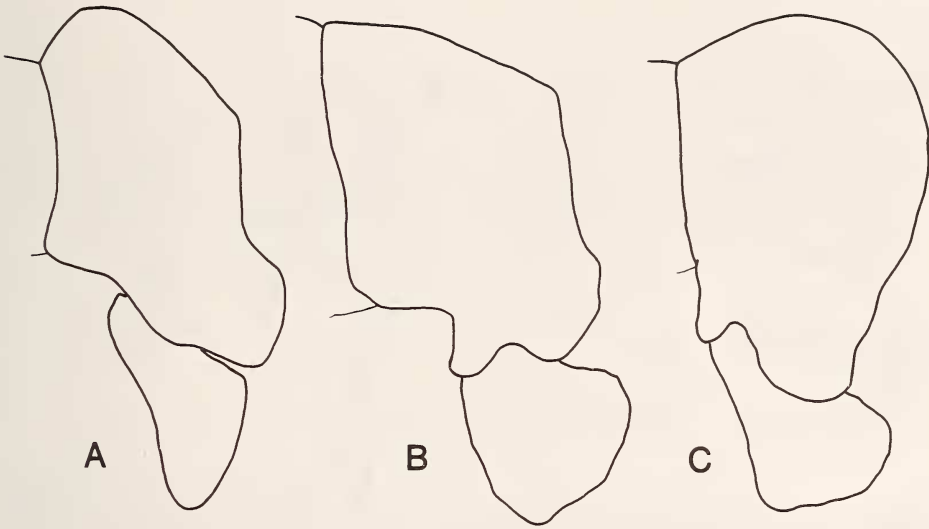


FIGURE 4. Epandrium, surstylus, and cercus, lateral view: A - *L. atra*, Sweden; B - *L. norrbomi*, Nepal; C - *L. bicolor*, Nepal.

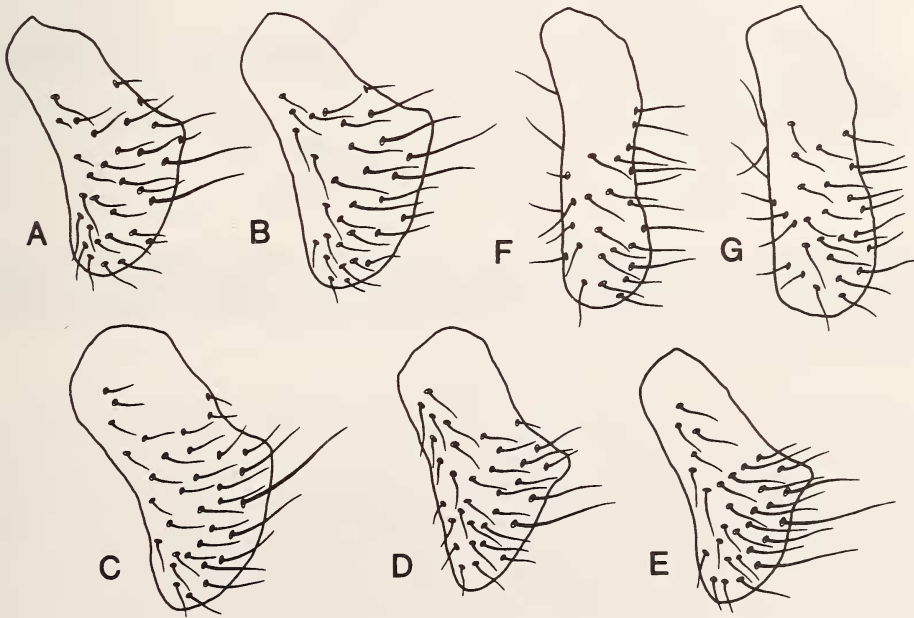


FIGURE 5. Left surstylus, lateral view: A - *L. atra*, Sweden; B - *L. atra*, Crete; C - *L. confusa*, China, Szechwan; D - *L. confusa*, U.S.A., Arizona; E - *L. confusa*, U.S.A., Alaska; F - *L. pallida*, Japan, Shikoku; G - *L. pallida*, Japan, Hokkaido.

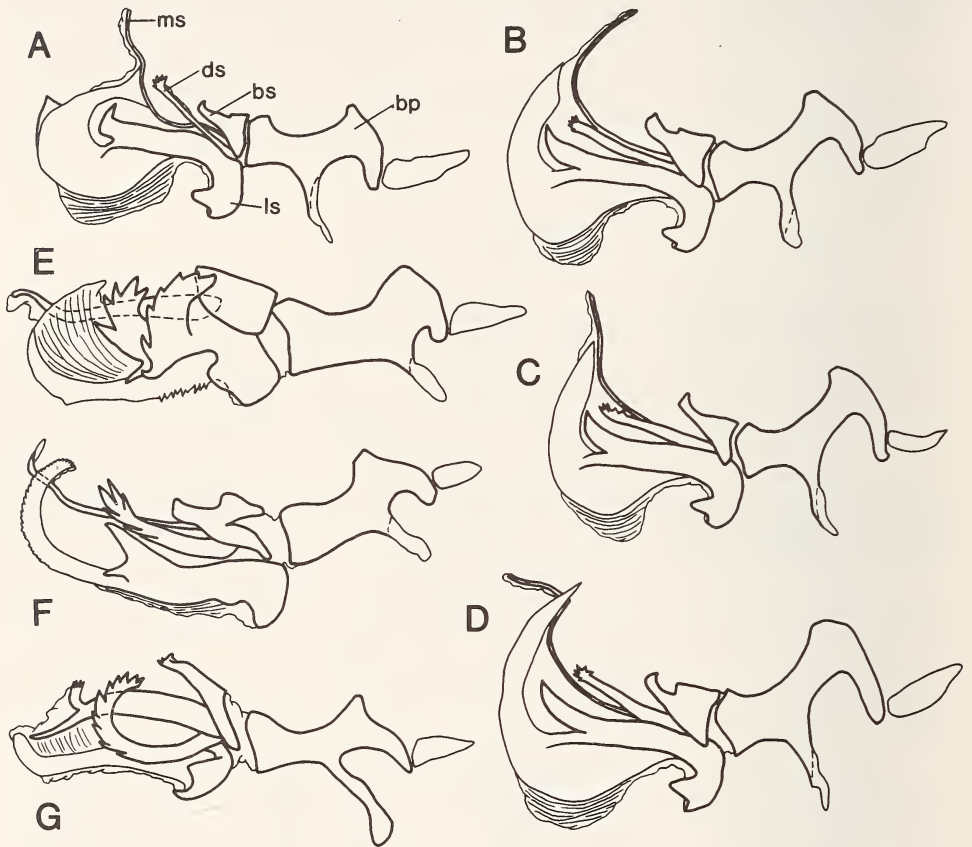


FIGURE 6. Aedeagus, left lateral view: A – *L. atra*, Sweden; B – *L. confusa*, Mexico, Mexico; C – *L. confusa*, U.S.A., Alaska; D – *L. confusa*, China, Szechwan; E – *L. norbomi*, Nepal; F – *L. pallida*, Japan, Shikoku; G – *L. bicolor*, Nepal; bp – basiphallus; bs – basal sclerite; ds – dorsally projecting sclerite; ls – lateral sclerite; ms – medial sclerite.

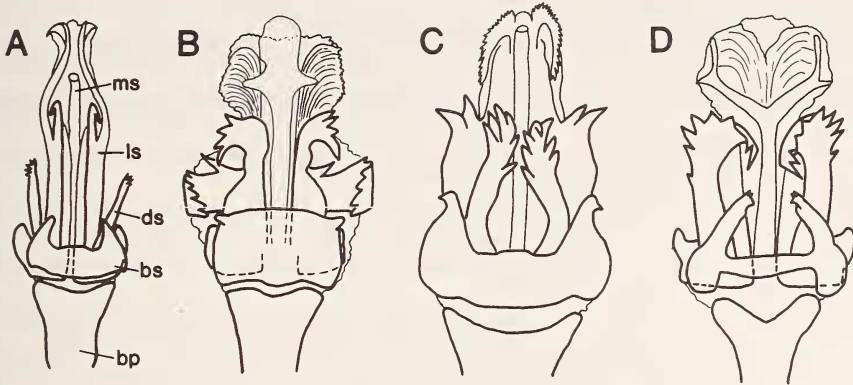


FIGURE 7. Distiphallus, dorsal view: A - *L. atra*, Sweden; B - *L. norrbomi*, Nepal; C - *L. pallida*, Japan, Shikoku; D - *L. bicolor*, Nepal; bp - basiphallus; bs - basal sclerite; ds - dorsally projecting sclerite; ls - lateral sclerite; ms - medial sclerite.

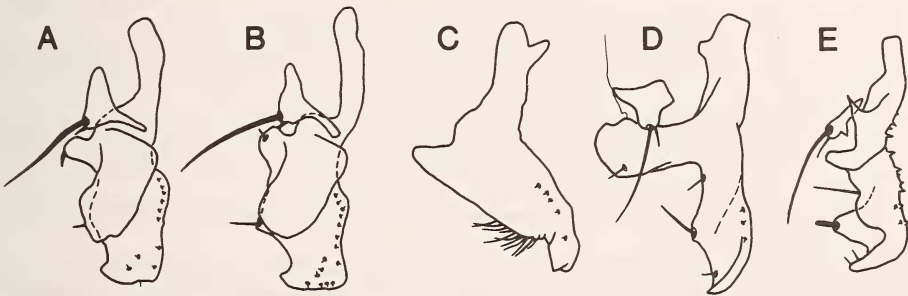


Figure 8. Left paramere, lateral view: A - *L. atra*, Sweden; B - *L. confusa*, Mexico, Mexico; C - *L. norrbomi*, Nepal; D - *L. pallida*, Japan, Shikoku; E - *L. bicolor*, Nepal.

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